

SCIENCE

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THE GEOLOGICAL AND FAUNAL RELATIONS OF EUROPE AND AMERICA DURING THE TERTIARY PERIOD AND THE THEORY OF THE SUCCESSIVE INVASIONS OF AN AFRICAN FAUNA.*

SEVERAL years ago the discovery of some new types of Rhinoceroses in this country directed my attention afresh to the study of the Tertiary fauna of Europe as parallel with that of America. In the succession of European and American types it appeared that there were most interesting similarities between rhinoceroses as widely separated as the present regions of Colorado and Southern France, but upon attempting more than a general comparison I was confronted by a lack of definite time scale between the levels in which these animals occur. The available correlations by Cope, Filhol, Scott, Zittel and others proved too indefinite at certain points. This difficulty became so obstructive that a more exact correlation of European and American horizons appeared to be an essential basis not only for the phylogeny of the Rhinoceroses but for that of other types of mammals of Europe and North America.

STRATIGRAPHICAL CORRELATION.

In an address before the Academy last year the various steps which have been taken to secure such correlation were described. The work proves to be a very diffi-

*Address of retiring President, New York Academy of Sciences, February 26, 1900.

cult one and is by no means complete. The kind co-operation of the leading paleontologists of Europe was enlisted and as a result an approximate correlation sheet was prepared. This was virtually a report of progress in this investigation, main emphasis being laid upon geological succession. In continuing the subject this year, main emphasis will be laid upon *faunal* succession or the distribution of the different orders and families of mammals, concluding with the latest views as to the succession of life during the Pleistocene period in Europe.

IYELLS SYSTEM			Approximate American Parallels	
PLEISTOCENE	UPPER	Post Glacial & Recent		
	MIDDLE	Glacial & Interglacial		
	LOWER	PREGLACIAL	7EQUUS BEDS	
PLEIOCENE	UPPER	SICILIEN	7BLANCO	
	MIDDLE	ASTIEN		
		PLAISANCIEN		
MIOCENE	LOWER	MESSINIEN	Upper Loos Fork	
	UPPER	TORTONIEN	LOUP FORK	
	MIDDLE	HELVETIEN	Lower Loos Fork	
OLIGOCENE	LOWER	LANGHIEN	Upper John Day	
		AQUITANIEN	Lower John Day (Diceratherium Layer)	
	UPPER	STAMPIEN	WHITE RIVER	
EOCENE	LOWER	INFRA-TONGRENIEN		
	UPPER	LIGURIEN	BRIDGERAUNTA	
	MIDDLE	BARTONIEN	LOWER BRIDGER	
		LUTETIEN	WIND RIVER	
	LOWER	SUESSONIEN	WASATCH	
BASAL		THANETIEN	TORREJON	
		MONTIEN	PUERCO	

CHART I.—Preliminary Correlation Table of European and American Tertiary Horizons. On all the levels above the Stampien the parallels are imperfectly established.

The preliminary correlation sheet abbreviated in Chart I. sets forth the results of the geological succession and correlation so far as it has been carried at present and illustrates the rapid progress of our knowledge of our own horizons. It includes the latest results of the American Museum explorations in the Miocene of Colorado and Kansas, as roughly studied by Matthew, but these correlations are not to be under-

stood as final. Scott has already transferred our John Day of Oregon, from the Miocene, where it was formerly placed, to the Upper Oligocene. The lower part at least of these beds belongs in the Oligocene—while the Upper John Day may prove to correspond with the Lower Miocene of Europe. Our Pliocene record as compared with the magnificent Pliocene of Europe is extremely meagre and our Miocene succession rich as it is, is not as fully understood as the Miocene of France. We look for more exact results from the American Museum explorations which are now being collated. It is only when we pass into the great time period from the Oligocene downwards that the American record becomes a superbly complete time standard for the whole Northern Hemisphere or Holarctic Region.

TERTIARY GEOGRAPHICAL DISTRIBUTION.

The importance of geographical distribution was first recognized by Humboldt, and set forth by Darwin in the 'Origin of Species,' in 1858. In the same year Selater divided the world into eastern and western divisions or Palaeogæa and Neogæa, to embrace the Old and New Worlds respectively, a division which has proved to be totally illogical. This led Darwin's distinguished colleague, Alfred Wallace, to his great work upon the 'Geographical Distribution of Animals' and the division of the world into life regions; in which Selater's scheme was adopted and developed.* In 1868, Huxley divided the world into a northern division, Arctogæa, and a southern division Notogæa to include the Northern and Southern Hemispheres respectively; this division was a little nearer the truth than Selater's. Between 1868 and 1890,

* The history of opinion upon this subject is fully set forth by Lydekker's invaluable work the 'Geographical Distribution of Mammals,' published in 1896.

Selater, Allen, Newton and Blanford, working upon living birds and mammals, continued this investigation, but it remained for Blanford, in 1890, to prove that the world zoologically should be divided into three great divisions; an Australian, a South American and a third region, *Arctogæa*, comprising North America, Europe, Asia and Africa.

Now it is clear that exactly as our understanding of the relations of living animals and plants to each other depends upon their fossil ancestors or upon their paleontology, so the final test of a scheme of zoological distribution must be a paleontological test. The animals of various families and orders have either originated in or migrated into their present habitat in past time, so that the geological record as to their order of appearance becomes of first importance. Here again the necessity of an *absolutely reliable correlation time scale* such as we are now establishing becomes evident, for the very first step toward an exact solution of the problem of past migration is to establish, as far as possible, the faunal parallels upon different continents, we can then determine where certain types of animals first appeared, and distinguish between the autochthonous endemic or native types and the migrant or new types.

This then is our problem, to connect living distribution with distribution in past time and to propose a system which will be in harmony with both sets of facts.

The tests of synchronism between European and American depositions are fourfold: First, the presence of a number of identical or closely allied genera and species. Second, similarity in the steps of evolution in related animals. Third, the predominance and spread of certain animals, as of the odd-toed Ungulates in the middle Eocene and of the even-toed Ungulates in the Upper Eocene. Fourth, the sudden

appearance of new types which have apparently originated elsewhere and have enjoyed an extensive migration, so that they appear simultaneously in different regions of the earth. An instance of this kind is afforded by the unheralded appearance of new types in the base of the Oligocene (*Rhinoceroses*) and of the Miocene (*Proboscidea*) in Europe and America.

Unfortunately there is still no agreement among zoologists as to the faunal geographical divisions. Lydekker, well versed in both paleontology and zoology, has for the first time brought together both classes of evidence in his recent valuable work upon the 'Geographical Distribution of Mammals'; he shows conclusively that zoo-paleontology favors the division of the world into three great realms as proposed by Blanford, to these may be applied the terms *Arctogæa*, *Notogæa* and *Neogæa*, as proposed anonymously in 1893. (Chart II.)

Geographically, these realms are connected by low lying portions of the earth, which, during long periods of submergence beneath the sea, have completely isolated them. At the same time we are forced to conclude that there were shorter intervals of elevation or land continuity at various times during the Tertiary period.

Now it is a well-known principle of zoological evolution that an isolated region, if large and sufficiently varied in its topography, soil, climate and vegetation, will give rise to a diversified fauna according to the *law of adaptive radiation** from primitive and central types. Branches will spring off in all directions to take advantage of every possible opportunity of securing food. The modifications which animals undergo in this adaptive radiation are largely of mechanical nature, they are lim-

*So termed by the writer, see 'Rise of Mammalia in North America,' 1893, and 'Origin of Mammals,' 1898.

ited in number and kind by hereditary, stirp or germinal influences, and thus result in the independent evolution of similar types in widely-separated regions under the law of parallelism or homoplasy.

This law causes the independent origin not only of similar genera but of similar families and even of our similar orders. Nature thus repeats herself upon a vast

above orders, and the Hystricomorph rodents enjoyed their chief radiation. In *Notogaea* two orders were cut off by the sea, one of them a rapidly declining type, the Monotremes, the other the Marsupials enjoying a very highly diversified radiation. This hypothesis is expressed in Chart IV. Two other orders of mammals, the Sirenia (probably a branch of the hoofed tribe), took the

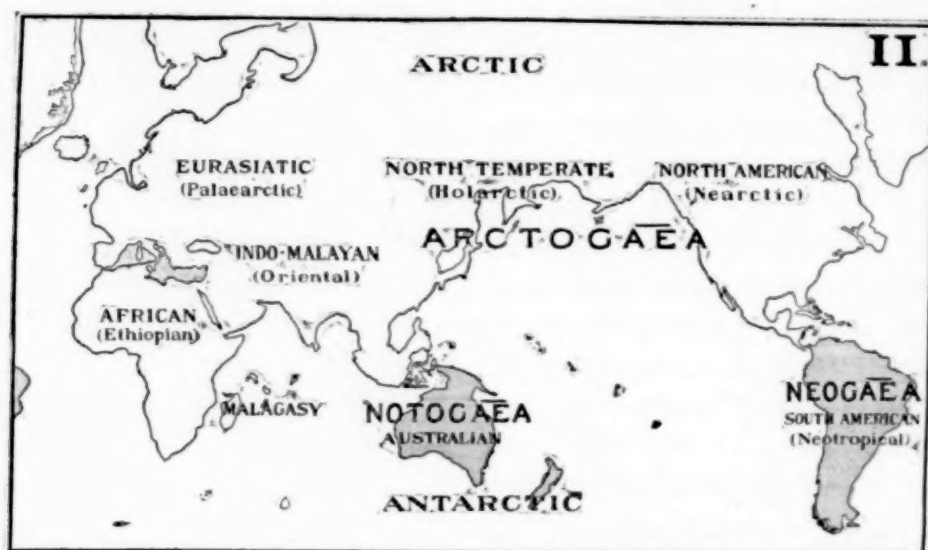


CHART II.—Division of the World into three Realms and nine main Geographical Regions. The continental platform is raised to the 200 metre line showing the main Tertiary land connections.

scale, but the similarity is never complete and exact. When migrations are favored by over-population or geographical changes, a new and severe test of fitness arises by the mingling and competition of the parallel types.

Now under the operation of these laws a most interesting generalization or hypothesis can be made as to the three realms, geographical isolation has been so continuous and prolonged that great orders of mammals have been evolved (Chart IV.) in each. Thus *Arctogaea* containing the broadest and most highly diversified land area, appears hypothetically as the center in which fourteen primitive and specialized orders radiated from each other. In the southern portion of *Neogaea*, at least four orders sprang from primitive members of the

rivers and coasts of America, Europe and probably Africa as their radiating center, while the Cetacea occupied the fourth or oceanic realm.

Now, we mean to express by this hypothesis that *Realms* were the main centers of adaptive radiation of orders, by no means the exclusive areas of distribution, for during the periods of land contact certain members of these orders found their way into adjacent realms. Each realm, therefore, contains its pure autochthonous types and its migrant or derived types. *Regions*, on the other hand, may be distinguished from realms as geographical and zoological areas, which have been isolated from each other for shorter periods, either by climatic barriers, as in the case of the Arctic or circumpolar region, or by great physical bar-

riers, such as masses of water and of desert sands. In certain cases these regions, such as Africa, appear to have been so large, distinct and isolated as to have become important centers of the radiation of certain orders of mammals, and almost attain the rank of realms, but regions in general are chiefly and permanently distinguished by the *adaptive radiation of families of mammals*.

Arctogæa may thus be still divided on the old lines into five or six regions, the *Arctic* or Circumpolar; the *Ethiopian* or African, south of the Sahara; the *Indo-Malayan* or Oriental, including southern Asia and the Malayan islands; the *Malagasy*, including Madagascar; the *Neartic* and the *Palæarctic*. There is no question, as suggested by Professor Newton in his term 'Holarctic,' and by Professor Allen in 1892, in his term 'North temperate,' that the North American (Neartic) and Eurasiatic (Palæarctic) regions are now so closely similar that they might be united into one. When, however, the zoological or existing characteristics of these regions are put to a paleontological test it is found necessary to separate them, because throughout the Tertiary period North America and Eurasia were so remote that, to a certain extent, they constituted centers, not only of independent family, but to a limited degree of ordinal radiation. At the same time they were unified, both by frequent intermigrations and by a simultaneous evolution of allied animals.

We now come to one of the greatest triumphs of recent biological investigation, namely, the concurrence of botanical, zoological and paleontological testimony in the reconstruction of a great southern continent to which the name Antarctica has been given. Following Blanford (1890), in 1893 Forbes* made the first strong plea for this continent. The flood of evi-

dence for the Antarctica theory has now become so strong that only a few details can be mentioned: Forbes (1893) and Milne-Edwards from the consideration of the birds; Beddard (1895) from the study of worms and other invertebrates; Moore (1899) from the study of the flora of South Africa; Spencer (1896) from the study of the fauna of Australia; Ameghino, Hatcher, and Ortmann from studies and collections of vertebrate and invertebrate fossils in Patagonia not yet fully published; Moreno (1899) from the discovery of *Miolania*, an Australian fossil reptile recently found in South America. From these and many other sources has been brought forth the body of testimony which draws us almost irresistibly* to the conclusion that there was an Antarctic continent at various times connecting South America, South Africa, Australia and New Zealand. Such a connection strengthens Huxley's conception announced in 1868, that the zoological regions were mainly upon lines of latitude, rather than as suggested by the present configuration of the earth, upon lines of longitude. With the theoretical elevation of this submerged continent (Chart III.) which may be called the 'Antarctic Region,' so as to connect the southern land masses at various times, all present and past geographical distribution may be theoretically accounted for. Elevation to the 10,000 foot (3040 meter) line still leaves a broad channel south of Africa. Without such elevation we are still met by many insuperable difficulties.

Among other problems, a land connection between Africa and South America across the South Atlantic enables us to explain the remarkable distribution of the sirenias, sea-cows, dugongs and manatees, now found exclusively in the tropical belt of Africa and the Americas. (See Sirenias, Chart

* H. O. Forbes, *Geographical Journal*, 1893. Also *Natural Science*, 1893, p. 54.

* After discussing the evidence with great fairness Lydekker (1896) takes a more conservative position.

evolution. The *Monotremes* also may have entered NOTOGÆA by either of these routes.

North America is the only part of the globe where Cretaceous mammals are known at present. In the late Cretaceous we appear to discover evidence of the existence

believed to be related to the HYRACOIDEA, upon the affinities of these forms turns the problem whether South America derived the sources of its great radiation from Africa or from South America. (See Chart IV.)



CHART IV.—Order of Mammals placed in their hypothetical chief centers of adaptive radiation during the Tertiary Period.

of the following orders: Insectivora, Creodonta or ancestral Carnivores, hoofed animals or Amblypoda and perhaps the earliest Monkeys or Mesodonta. In the basal Eocene we certainly find primitive Monkeys or Mesodonta; Rodentia and Tæniodontia or ancestral Edentata. A land connection with South America in the early Eocene would therefore have supplied *Neogaea* with the Edentates as well as the stem forms from which might have been derived its wonderful radiation of hoofed animals—the Litopterna, Typotheria and Toxodonta; together with the remarkable radiation of the Hystricomorph or porcupine-like rodents and of two families of Monkeys.

The exact zoological affinities of the oldest mammalian or *Pyrotherium* fauna of South America remain to be determined. *Pyrotherium* itself is considered by Ameghino (1895) as the source of the order PROBOSCIDA while other ungulates are be-

lieved to be related to the HYRACOIDEA, upon the affinities of these forms turns the problem whether South America derived the sources of its great radiation from Africa or from South America. (See Chart IV.)

Four streams of migration to and from NEOGÆA appear to have occurred; the first established its autochthonous fauna or distinctive radiation of peculiar ungulates and edentates. The second related this region with Africa, via Antarctica; this contact, in addition to the problematical Proboscidea and Hyracoidea above alluded to, apparently introduced stem forms of Edentates into the Ethiopian region from which were derived the Pangolins and Aard Varks; these peculiar edentates together with Armadillos all occur in southern France in the lower Oligocene (Fihol, 1893); this land bridge also distributed the Cape Golden moles, *Chrysochloridæ*; these facts and others too numerous to mention serve to show the vast importance of the explorations in Patagonia and make us impatient for the exact conclusions which are forthcoming from the materials brought together by Ameghino and Hatcher.